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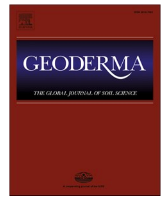

Belowground allocation and fate of tree assimilates in plant–soil–microorganisms system: ^{13}C labeling and tracing under field conditions

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A R T I C L E I N F O

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A B S T R A C T

Although forests account for only 27% of the total land area, they store approximately 80% of the aboveground carbon (C) and 40% of soil C globally. However, there is currently little information regarding the input and distribution of photoassimilates of trees in plant–soil systems. To quantify the belowground C input and allocation to plant–soil pools, we pulse labeled 5-year-old pioneer (*Populus davidiana*) and climax (*Quercus wutaishanica*) species with $^{13}CO_2$ under field conditions. The ^{13}C allocation dynamics were traced in the leaves, branches, roots, and soil microorganisms, rhizosphere and bulk soil under *Populus davidiana* and *Quercus wutaishanica* over 21 days. ^{13}C recovery (% of assimilated ^{13}C) in the leaves of *Populus davidiana* and *Quercus wutaishanica* decreased from nearly 90% at 6 h after labeling to 40% and 45% at 21 days, respectively. Continuous assimilate allocation from above- to belowground increased ^{13}C recovery in roots from 0.4% at 6 h after labeling to 9.5% in *Populus davidiana* and from 1.5% to 15% in *Quercus wutaishanica* at 21 days after labeling. The recently assimilated C was detected in the soil immediately after labeling. The ^{13}C amounts in the bulk and rhizosphere soil of the climax species *Quercus wutaishanica* was two-fold greater than that under the pioneer species *Populus davidiana.* The total belowground net C input (including that in roots) by *Populus davidiana* and *Quercus wutaishanica* was 109 and 283 g C m^{-2} yr^{-1} (top 20 cm of soil), respectively, including rhizodeposition of 4.2 and 28 g C m^{-2} yr^{-1}. Consequently, the belowground C allocation and soil C sequestration increase from pioneer to climax tree species.

1. Introduction

Globally, approximately 60 Pg yr^{-1} carbon (C) in biotic pool (wood and non-wood plants), is transferred into the soil (1 m depth) mainly via roots and rhizodeposition as well as from litter-fall decomposition (Lal, 2008; Peh et al., 2015). The rhizodeposition of organic C is one of the primary pathways that links the plant–soil system and influences soil C cycling (Finzi et al., 2015; Chomel et al., 2019). Root-released C provides energy for rhizosphere microbial communities, thereby shaping their structure and functions, and thus driving distinct C sequestration processes (Strand et al., 2008; Pausch and Kuzyakov, 2018). Despite the importance of root C in soil C cycling, the methodology necessary to measure rhizodeposition remains challenging, thus highlighting the need for further studies examining strategies for determining amounts of C deposited in the rhizosphere.

Forests store almost 90% of the global biomass C, with 74 t ha^{-1} of C being stored in forest soils (Peh et al., 2015). Consequently, even small changes in C allocation of trees in plant–soil systems could have a

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Table 1
Basic information of the plots and trees for ^{13}C labeling.

Plantation types	Site number	Longitude (°)	Latitude (°)	Altitude (m)	Mean tree height (m)	Mean diameter at breast height (cm)
Populus davidiana	1	109°10′15″	36°04′24″	1188	3.0 ± 0.7	15 ± 0.5
	2	109°10′36″	36°04′44″	1190	3.1 ± 0.5	16 ± 0.6
	3	109°09′54″	36°04′32″	1195	3.1 ± 0.3	17 ± 0.7
Quercus wutaishanic	1	109°10′17″	36°04′47″	1186	3.8 ± 0.7	16 ± 0.3
	2	109°10′48″	36°04′41″	1186	3.7 ± 04	14 ± 0.4
	3	109°10′14″	36°04′36″	1184	3.9 ± 0.3	15 ± 0.4

pronounced influence on terrestrial ecosystem C balance (Bonan, 2008; Reichstein et al., 2013). Photosynthetic-assimilated CO_2 is the primary source of organic C input to soil. However, progress on the study of C cycling tends to be hampered by the scarcity of field data necessary for the purposes of modeling, particularly with respect to the dynamics of C allocation in trees (Kuzyakov and Gavrichkova, 2016). Given the interest in storing increasing amounts of C in forests to promote C sequestration, gaining an in-depth understanding of the fluxes and dynamics of newly assimilated C above- and belowground is considered a research priority.

Currently, the most common approach to analyze C allocation and transformation in plant–soil systems is $^{13}CO_2$ pulse labeling (Sanaullah et al., 2012; Pausch and Kuzyakov, 2018; Zang et al., 2019). This method has been used to explore the turnover rate of C pools with various structures and functions, such as soil microbial biomass C (MBC) and extractable organic C (EOC) (Ge et al., 2015; Haddix et al., 2016), in grasslands (Allard et al., 2006; Schmitt et al., 2013) and croplands (Pausch et al., 2013; Zang et al., 2019). Using a $^{13}CO_2$ pulse labeling approach, researchers estimated that the net rhizodeposition for crops and grasslands was ranged from 16 to 33 g C m^{-2} yr^{-1} from 8.8 to 55 g C m^{-2} yr^{-1}, respectively (Loya et al., 2002; Pausch and Kuzyakov, 2018; Zang et al., 2019). In forests, approximately 1%–10% of the total assimilated photosynthetic C is lost to exudation, which is notably lower than that recorded for crops (20%–30%) and grasslands (30%–50%), but tree species dependent (Qiao et al., 2014; Pausch and Kuzyakov, 2018; Zang et al., 2019). The findings indicate that C allocation in plant–soil systems is strongly dependent on plant species, which represents a primary factor accounting for the uncertainty associated with estimates of newly assimilated C based on $^{13}CO_2$ or $^{14}CO_2$ labeling.

Tree species can be classified as either pioneer or climax types depending on their respective regeneration characteristics (Swaine and Whitmore, 1988). Pioneer species are generally characterized by a higher light-saturated rate of photosynthesis than climax species. However, the leaves of climax species typically have a higher quality per unit area and higher chlorophyll to nitrogen ratio, which tend to be more conducive to the synthesis of more structural and pigment compounds than in pioneer species (Valladares and Niinemets, 2008). Currently, it remains unclear as to whether it is pioneer or climax species that absorb more photosynthetic C. Nevertheless, differences in the ecological strategies and photosynthetic activities of pioneer and climax species would tend to imply potential differences in the contributions of root lysates and exudates to rhizodeposition and the ratio of rhizodeposition C to root C (Koyama, 1978).

In order to examine the allocation patterns of newly assimilated C in above- and belowground pools in climax and pioneer species, we selected *Populus davidiana* and *Quercus wutaishanica* as the pioneer and climax species, respectively, to perform *in situ* $^{13}CO_2$ pulse labeling. As primary objectives, we assess the following hypotheses: (1) compare with a pioneer tree species (*Populus davidiana*), the leaves of a climax tree species (*Quercus wutaishanica*) fix more photosynthetic C, thereby leading to higher rhizodeposition into the soil and higher ratio of the total assimilated photosynthetic C to exudation C; and (2) for both *Populus davidiana* and *Quercus wutaishanica*, recent photosynthetic C transfer from leaves to roots, and even to the soil immediately after labeling.

2. Materials and methods

2.1. Study site

The Loess Plateau in China is one of the most severely eroded regions in the world, as a consequence of reduced vegetation coverage (Liu et al., 2014). In an effort to restore the forest cover and prevent soil erosion on sloped croplands in this region, during the 1990s, the Chinese government implemented the "*Grain for Green*" project. And after 30 years of revegetation, marked increases in plant cover and diversity had been recorded (Liu et al., 2014). The present study was conducted on the Ziwuling Mountain, Yan'an City, Shannxi Province (36°03′52″–36°04′49″N, 109°09′54″–109°10′48″E), which support the largest existing natural secondary forest on the Loess Plateau (Fig. S1, Table. 1) that has been established for approximately 160 years. The mean annual rainfall and temperature of the study area are 500–600 mm and 7.4–9.3 °C, respectively, the frost-free period of approximately 124–140 days. According to the WRB soil taxonomy, the zonal soil type is a Cambisol. The primary forest species are *Robinia pseudoacacia, Platycladus orientalis, Populus davidiana*, and *Quercus wutaishanica*, with the succession from *Populus davidiana* to *Quercus wutaishanica* in this region occurring over a period of approximately 50 years (Li and Shao, 2004).

2.2. $^{13}CO_2$ pulse labeling

$^{13}CO_2$ labeling was conducted on July 27th, which coincided with a period of sunny weather extending for at least three consecutive days. As labeling sites, we selected three sites with a coverage of *Populus*

Table 2
Soil physical properties under *Populus davidiana* and *Quercus wutaishanic*.

Tree species	Study site	Soil pH		Soil bulk density		Soil texture					
						Clay (%)		Silt (%)		Sand (%)	
		0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm	0–10 cm	10–20 cm
Populus davidiana	1	7.8 ± 0.1	7.9 ± 0.4	0.9 ± 0.2	1.1 ± 0.1	12 ± 1.1	13 ± 1.1	68 ± 4.2	69 ± 7.4	20 ± 2.1	18 ± 2.1
	2	7.9 ± 1.1	8.0 ± 0.1	1.1 ± 0.1	1.2 ± 0.3	13 ± 0.4	13 ± 0.4	73 ± 5.1	71 ± 6.5	14 ± 1.2	16 ± 1.8
	3	8.0 ± 0.1	8.0 ± 0.5	1.0 ± 0.2	1.0 ± 0.1	11 ± 2.1	12 ± 2.1	77 ± 2.5	78 ± 6.8	12 ± 1.1	10 ± 0.7
Quercus wutaishanic	1	7.7 ± 0.2	7.8 ± 0.1	0.9 ± 0.1	1.0 ± 0.2	12 ± 1.3	12 ± 1.3	77 ± 4.4	78 ± 4.4	11 ± 0.9	10 ± 0.6
	2	7.8 ± 0.3	7.9 ± 0.4	1.0 ± 0.2	1.1 ± 0.2	13 ± 1.3	14 ± 1.3	79 ± 3.5	80 ± 5.8	8.0 ± 0.7	6.0 ± 0.2
	3	7.9 ± 0.4	7.9 ± 0.4	1.0 ± 0.1	1.1 ± 0.1	12 ± 2.3	13 ± 2.3	81 ± 2.5	80 ± 7.4	7.0 ± 0.5	7.0 ± 0.5

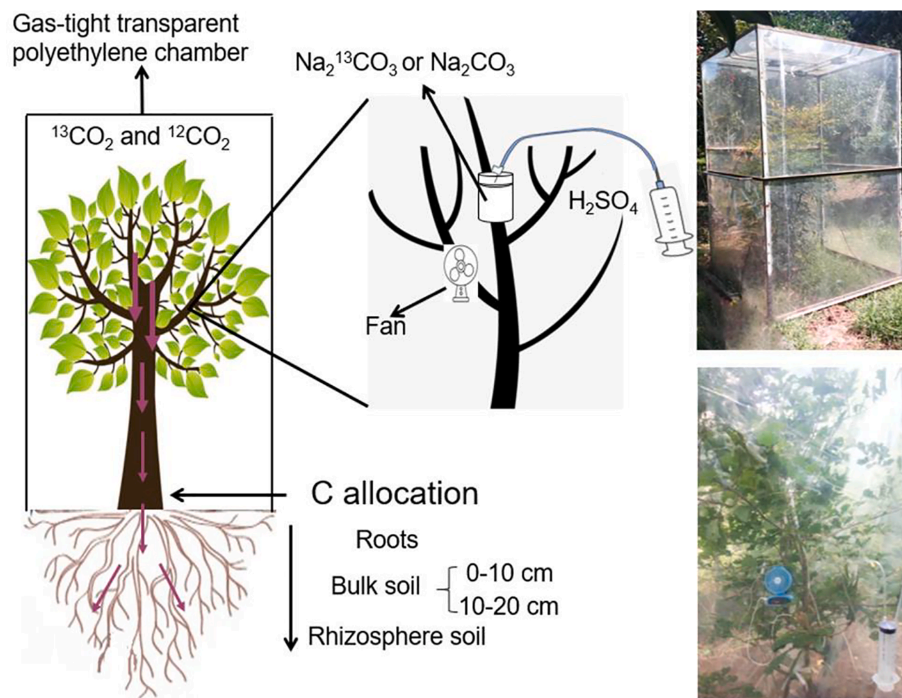

Fig. 1. The experimental set-up used for $^{13}CO_2$ pulse labeling of *Populus davidiana* and *Quercus wutaishanica*.

davidiana and three with a cover of *Quercus wutaishanica* (30 m × 30 m, at least 1 km apart), characterized by similar soil type, elevation, latitude, and longitude. The basic physical properties of the soil are shown in Table 2. At each site, we selected four *Populus davidiana* or four *Quercus wutaishanica* specimens, which were of approximately similar age (5 years) and height (3–4 m) and separated by a distance of at least 10 m. Thus, a total of 24 trees (12 *Populus davidiana* and 12 *Quercus wutaishanica*) were selected. Of the four trees at each site, three were selected for ^{13}C pulse labeling, with the fourth being used as an unlabeled reference tree. Prior to labeling, all vegetation (i.e., grasses and shrubs) growing beneath the trees were cleared to prevent ^{13}C fixation, and the soil was sealed with plastic foil to minimize the diffusion of $^{13}CO_2$ into the soil. The CO_2 concentration in each labeling chamber was measured using a TEL7001 infrared CO_2 analyzer (Telaire, USA), with labeling being commenced when the CO_2 concentration had dropped to 0.018%.

The gas-tight low-density polyethylene labeling chambers used in the present study were of dimensions 1.5 × 1.5 × 4.0 m, and permitted more than 90% transmittance of photosynthetically active radiation (Fig. 1). ^{13}C was applied as $^{13}CO_2$ to the aboveground parts of the plants by simultaneously pulse-labeling trees in each of the 18 individual chambers. The $^{13}CO_2$ was released by mixing $Na_2^{13}CO_3$ (99 atom% ^{13}C, Berlin, Germany) with H_2SO_4. In each chamber, four fans were installed at different positions to ensure the even distribution of $^{13}CO_2$. Four 250 mL polyethylene bottles (three containing 21 g of $Na_2^{13}CO_3$ and one containing 21 g non-isotopically enriched analog Na_2CO_3) were fixed to the branches within chambers. The chambers were then closed and 100 mL of 1 M H_2SO_4 was introduced to a polyethylene bottle using a syringe at 1.5 h intervals (0, 1.5, and 3 h) over a period of 4.5 h. Finally, 300 mL of 1 M H_2SO_4 was added to the 21 g of $Na_2^{13}CO_3$ and we added 2400 mg of ^{13}C if the $Na_2^{13}CO_3$ and H_2SO_4 reacted completely. Following the final round of pulse labeling, a further 100 mL of 1 M H_2SO_4 was added to a polyethylene bottle containing Na_2CO_3 (21 g) to enhance the absorption of $^{13}CO_3$. The CO_2 concentration (0.06%–0.07%) and temperature (approximately 26 ℃) within the labeling chambers were similar to those detected by the infrared CO_2 analyzer during the 6 h (11:00–17:00) pulse-labeling period.

2.3. Plant and soil sampling

Given that the selected trees were a maximum of 4 m in height and taking into consideration the results obtained by Zang et al. (2019), Pausch and Kuzyakov (2018), and Remus et al. (2016), we assumed that 21 days would be a sufficient length of time to examine C allocation in the study plant–soil system. Plant and soil samples were collected at 0, 5, 12, and 21 days after labeling (day 0 corresponds to 6 h after commencing $^{13}CO_2$ labeling). Immediately after labeling, we collected unlabeled samples from the reference tree at each study site, which were at least 10 m distant from the labeled trees. Plant samples included leaves, branches (bearing leaves), and roots. From each labeled tree, we collected four leaf-bearing branches (approx. 3 cm in diameter), with sub-samples being collected from the inner, central, and outer parts of each tree canopy to obtain approximately 500 g of leaves and branches. Root and soil samples were collected at depths of 0–10 and 10–20 cm using a root auger (5 cm in diameter; three replicates for each tree) with a rubber hammer at a distance of approximately 15 cm from the tree. The soil attached to the roots (approx. 3 cm diameter) was regarded as rhizosphere soil, and the remaining soil was treated as bulk soil. Any dead roots collected were removed. Following pulse labeling, we collected roots from unlabeled reference trees by digging, which enabled us to ensure that the roots collected from the labeled trees belong to *Populus davidiana* or *Quercus wutaishanica* or not. All samples were transferred to the laboratory within 24 h of collection (stored in a carry-on fridge at 4 °C).

In the laboratory, the soil loosely adhering to the fresh roots was carefully shaken from the roots by hand, and the roots were washed five times with distilled water. The root washings thus obtained were retained in beakers and these suspensions were shaken for 30 min. And the suspensions were filtered through 0.50 μm membrane filters to obtain the rhizosphere soil samples (Paterson et al., 1995). The labeled and unlabeled leaf, branch, and washed root samples were oven-dried at 105 °C for 15 min and then heated at 70 °C for 72 h to a constant weight in a small carry-on oven (Bao, 2000). In the laboratory, the dried plant samples were homogenized and passed through 1-mm sieves prior to analysis of leaf C, N, and P, root and branch C, and $\delta^{13}C$.

Labeled and unlabeled bulk and rhizosphere soil samples were stored

Table 3
Plant and soil properties of *Populus davidiana* and *Quercus wutaishanic*.

Tree species	Study site	Leaf C content ($g\ kg^{-1}$)	Leaf N content ($g\ kg^{-1}$)	Leaf P content ($g\ kg^{-1}$)	Shoot C content ($g\ kg^{-1}$)	Root C content ($g\ kg^{-1}$)	Root biomass ($g\ m^{-2}$)	Soil C content ($g\ kg^{-1}$)		
								0–10 cm	10–20 cm	Rhizosphere soil
Populus davidiana	1	459 ± 12.1	15.2 ± 1.1	2 ± 0.8	440 ± 21.1	438 ± 14.1	530 ± 14.4	17 ± 0.2	13 ± 0.4	18 ± 0.5
	2	429 ± 21.1	14.7 ± 0.1	1.9 ± 0.8	438 ± 20.1	435 ± 10.1	529 ± 15.4	16 ± 0.1	14 ± 0.5	17 ± 0.4
	3	435 ± 12.1	16.2 ± 1.1	1.8 ± 0.8	437 ± 19.1	440 ± 12.1	531 ± 10.4	17 ± 0.5	13 ± 0.8	18 ± 0.6
Quercus wutaishanic	1	474 ± 11.2	17.1 ± 1.1	2.2 ± 0.2	449 ± 13.2	456 ± 15.3	600 ± 16.5	20 ± 0.4	14 ± 0.4	21 ± 0.9
	2	474 ± 11.2	17.1 ± 1.1	2.3 ± 0.2	451 ± 12.2	460 ± 14.3	604 ± 26.5	19 ± 0.5	14 ± 0.8	22 ± 1.2
	3	474 ± 11.2	17.1 ± 1.1	2.1 ± 0.2	452 ± 11.2	450 ± 16.3	610 ± 21.5	21 ± 0.5	15 ± 0.4	23 ± 2.1

in a refrigerator at 4 °C and transferred to the laboratory within 3 days of collection. Any adhering debris and macroinvertebrates within the fresh bulk soil samples (both labeled and unlabeled samples) were carefully removed using forceps. The bulk soil and filters with retained rhizosphere soil were divided into two portions, one of which was stored at −20 °C (within 1 week) for the analysis of soil microbial biomass (MBC) and extractable organic C (EOC), and the other was air-dried and passed through 0.15-mm sieves for analysis of $\delta^{13}C$. Prior to $\delta^{13}C$ measurement, 1 M HCl was added to bulk and rhizosphere soil samples, which were shaken for 24 h to remove inorganic C (mainly soil carbonate mineral C formed during weathering of the soil parent rock) (Harris et al. 2001). The soil samples were then oven-dried at 105 °C for 12 h prior to the analysis of soil organic carbon (SOC) and $\delta^{13}C$.

2.4. Measurement of soil and leaf properties

For the measurement of leaf total P and N, 5 mL of H_2SO_4 was added to samples followed by overnight digestion. Thereafter, the samples were placed in an electric furnace, digested until the color of the solution had become black, and cooled to room temperature. Following the further addition of H_2O_2, the solution was digested by boiling, and the procedure was repeated until the solution became colorless. Total P and N were measured using colorimetric (UV spectrophotometer) and micro-Kjeldahl methods, respectively (Bao, 2000). The organic C and $\delta^{13}C$ contents of soil and plant samples were analyzed using an elemental analyzer (Elementar Vario PYRO cube, Germany) coupled to an isotope ratio mass spectrometer (IsoPrime 100 Isotope Ratio Mass Spectrometer, Germany).

Soil MBC was determined from fresh soil using the chloroform fumigation-extraction method (Brookes, 1985). Approximately 10 g of fresh soil was fumigated with chloroform for 24 h and then shaken with 40 mL of 0.5 M K_2SO_4 for 30 min. Similarly, the same amount of non-fumigated soil was extracted with 0.5 K_2SO_4. The non-fumigated extract was used to determine the level of EOC in the soil, and the MBC was calculated as the difference in the organic C content between the fumigated and non-fumigated soil extracts, with corrections using a conversion coefficient (k_{EC}) value of 0.45 (Eq. (2)) (Wu et al., 1990). The K_2SO_4 extracts (4 mL) were freeze-dried prior to ^{13}C abundance analysis.

$$Total\ ^{13}C assimilation = ^{13}C\ \ leaves + ^{13}C\ branches + ^{13}C\ roots + ^{13}C\ bulk\&\ rhizo\ soil \quad (7)$$

2.5. Calculations

Soil MBC and EOC were calculated using Eqs. (1) and (2), respectively, as follows:

$$OC_E(mg\ C\ kg^{-1}) = \frac{OC_D\ (mg\ C\ L^{-1}) \times\ DR}{soil\ dry\ weight\ (g)}$$

$$MBC = \frac{E_C}{K_{EC}}$$

where OC_E is the C content in the extracting solution; OC_D is the C content in the determination solution measured using a total organic C analyzer (Element high TOC II, Germany), DR is the dilution ratio, EC is the difference in the OC_E values fumigated and non-fumigated; and k_{EC} is the conversion coefficient (0.45). EOC is the OC_E in the non-fumigated extracting solution.

To calculate the amounts of ^{13}C incorporated into leaves, shoots, roots, rhizosphere, and bulk soil, we used the following equations:

$$\delta^{13}C = \left(\frac{R_{sample}}{R_{PDB}} - 1\right) \times\ 1000‰ \quad (3)$$

where R_{sample} is the $^{13}C/^{12}C$ ratio in the samples and R_{PDB} (0.011237) is the isotopic ratio of $^{13}C/^{12}C$ in Pee Dee Belemnite (PDB).

The $^{13}C_{atom\%\ excess}$ was calculated as follows:

$$^{13}C_{atom\%} = \left(\frac{R_{sample}}{R_{sample} + 1}\right) \times 100 \quad (4)$$

$$^{13}C_{atom\%\ excess} = ^{13}C_{atom\%\ labeled} - ^{13}C_{atom\%\ unlabeled} \quad (5)$$

where $^{13}C_{atom\%\ excess}$ represents the percentage of ^{13}C atoms among the total carbon atoms present in the labeled and unlabeled samples, respectively.

The content of ^{13}C incorporated into the plant and soil pools was estimated using Eq. (6) (during each sampling period) as follows:

$$^{13}C\ content\ (g/kg) = ^{13}C_{atom\%\ excess} \times C\ content\ (g/kg) \quad (6)$$

where $C_{content}$ refers to the C content in the leaves, branches, roots, rhizosphere, or bulk soil (Table. 3).

Total ^{13}C assimilation was calculated as the sum of the ^{13}C content in leaves, branches, roots, rhizosphere, and bulk soil as follows:

^{13}C recovery (% of assimilated ^{13}C) in all C pools (leaves, branches, roots, and soil) was calculated as the ^{13}C content on the sampling days after labeling (0, 5, 12, and 21 days) divided by the content of ^{13}C (in the leaves, branches, roots, and soil) immediately after labeling ($^{13}C_{t\ 1st\ rec}$,

Table 4
Plant and soil $\delta^{13}C$ of *Populus davidiana* and *Quercus wutaishanic.*

Tree species	Time after ^{13}C labeling	$\delta^{13}C$ of leaves (‰)	$\delta^{13}C$ of branches (‰)	$\delta^{13}C$ of roots (‰)	$\delta^{13}C$ of soil (‰)		
					0–10 cm	10–20 cm	Rhizosphere soil
Populus davidiana	0	568 ± 71	23 ± 2.1	−16 ± 2.5	−25 ± 1.5	−25 ± 1.9	−26 ± 0.2
	5	210 ± 14	143 ± 11	−14 ± 3	−22 ± 1.1	−25 ± 1.2	−25 ± 0.7
	12	60 ± 32	−7.1 ± 2.6	−13 ± 5	−26 ± 1.4	−26 ± 0.2	−25 ± 0.7
	21	4.2 ± 0.3	−6.5 ± 2.4	−11 ± 8.8	−26 ± 1.5	−26 ± 0.7	−25 ± 0.8
Quercus wutaishanic	0	1037 ± 86	103 ± 47	−22 ± 1.1	−24 ± 2.1	−24 ± 1.8	−25 ± 1.6
	5	312 ± 44	176 ± 11	−20 ± 3.3	−22 ± 1.9	−23 ± 1.6	−24 ± 1.8
	12	123 ± 41	138 ± 41	−11 ± 1.1	−25 ± 2.4	−24 ± 2	−24 ± 1.9
	21	68 ± 15	32 ± 1.1	−10 ± 0.3	−24 ± 2.1	−23 ± 1.2	−24 ± 1.4

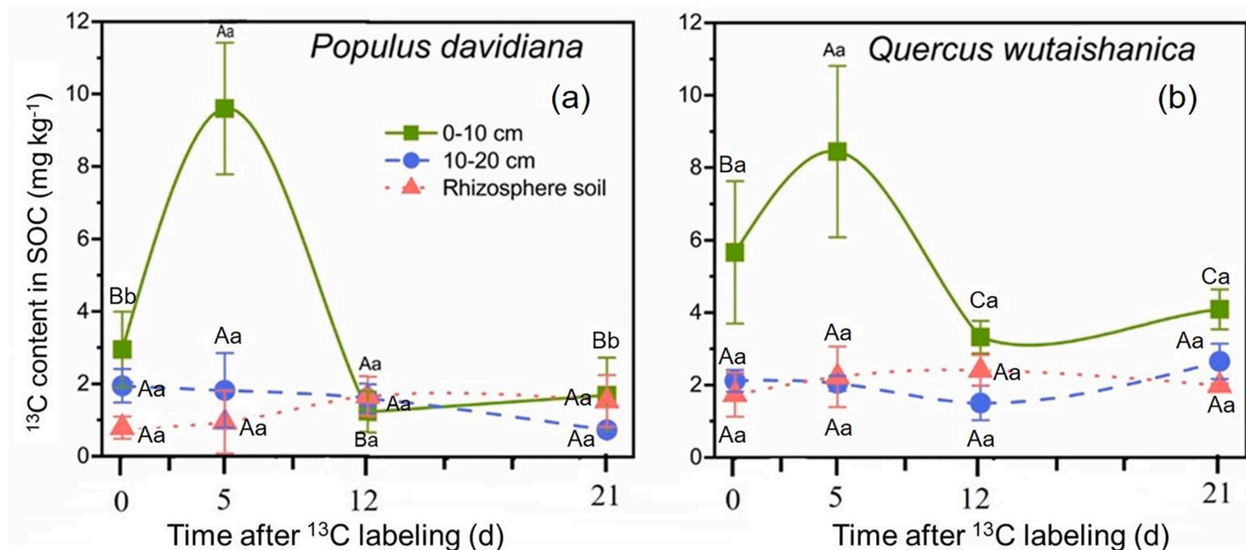

Fig. 2. ^{13}C content in soil organic carbon (SOC) of bulk soil (0–10 and 10–20 cm soil layers) and rhizosphere soil under pioneer species *Populus davidiana* and climax species *Quercus wutaishanica* trees at 0, 5, 12, and 21 days after pulse labeling in a $^{13}CO_2$ atmosphere. Values are the averages (±SD) of three replicates. Lowercase letters (a, b, and c) indicate significant differences ($p < 0.05$) between the two tree species for the same soil layer and same sampling time, and uppercase letters (A, B, and C) indicate significant differences ($p < 0.05$) between sampling times for the same soil layer. *Note*: Day 0 corresponds to 6 h after the commencement of $^{13}CO_2$ labeling.

%^{13}C of total added) (Liu et al., 2020).

$$^{13}C_{recovery}(\%) = \frac{^{13}C_{content}}{^{13}C_{t\ 1st\ rec}} \times 100 \quad (8)$$

The ^{13}C content in MBC was calculated using the following equation:

$$^{13}C\ contentMBC = \frac{\left(^{13}C_{atom\%\ fum\ label-}{}^{13}C_{atom\%\ fum\ unlabel}\right) \times C_{fum} - \left(^{13}C_{atom\%\ unfum\ label-}{}^{13}C_{atom\%\ unfum\ unlabel}\right) \times C_{unfum}}{100 \times 0.45} \quad (9)$$

where “fum” and “unfum” represent “fumigated” and “unfumigated” K_2SO_4 extracts, respectively, and C_{fum} and C_{unfum} are the amounts (mg kg^{-1} soil) of fumigated and unfumigated K_2SO_4 extracts, respectively.

First-order exponential decay functions were used to fit the ^{13}C decline in leaves (% of total assimilated ^{13}C) over the sampling time. The following formula was used to calculate the half-life and proportion of assimilated C remaining in the leaves:

$$N_t = a + N_0 * e^{-t} \quad (10)$$

where N_0 and N_t are the percentages of assimilated C in leaves at the time of maximum label incorporation and at time t, respectively, k is the rate constant, and a is the proportion of assimilated C remaining in the leaves. The half-life ($t1/2$) of C in leaves was calculated based on the rate constant $t1/2 = \ln(2)/k$.

2.6. Data analysis

All data are presented as the means ± standard deviation (SD), and all analyses were conducted using SPSS 22.0 (SPSS Inc., Chicago, IL, USA). The Shapiro-Wilk test was used to check for the normal distribution of residues, and homogeneity was determined using Levene’s test. Non-normally distributed data were initially log-transformed prior to statistical analysis. One-way ANOVA was used to compare the changes in ^{13}C of *Populus davidiana* or *Quercus wutaishanica* in the same plant component or same soil layer at different sampling times after pulse labeling. A *t*-test was used to compare the changes in ^{13}C in the plant and soil between the two species. Differences were considered

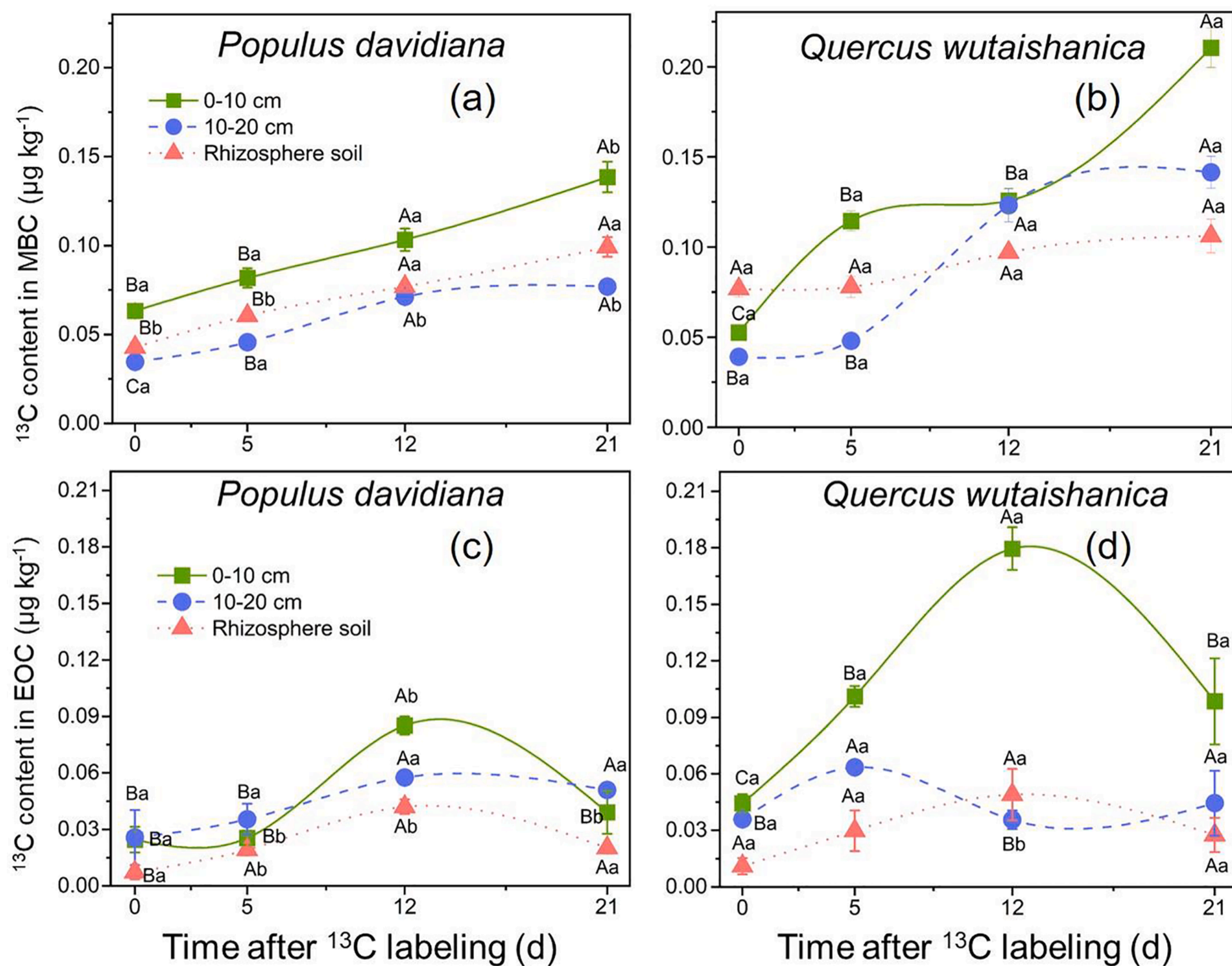

Fig. 3. ^{13}C content in microbial biomass C (MBC) and extracted organic C (EOC) in bulk soil (0–10 and 10–20 cm soil layers) and rhizosphere soil under pioneer species *Populus davidiana* and climax species *Quercus wutaishanica* at 0, 5, 12, and 21 days after the pulse labeling in a $^{13}CO_2$ atmosphere. Values are the averages (±SD) of three replicates. Lowercase letters (a, b, and c) indicate significant differences ($p < 0.05$) between the two tree species for the same soil layer and same sampling time, and uppercase letters (A, B, and C) indicate significant differences ($p < 0.05$) between different sampling times for the same soil layer or in rhizosphere soil. *Note*: Day 0 corresponds to 6 h after the commencement of $^{13}CO_2$ labeling.

statistically significant at $p < 0.05$. All charts were prepared using Origin Pro 2018 (Origin Lab Corporation).

3. Results

3.1. δ^{13}C in the plant–soil system after pulse labeling

Immediately after pulse labeling, leaf δ^{13}C reached to 568‰ and 1037‰ in *Populus davidiana* and *Quercus wutaishanica*, respectively, and thereafter declined with the time after labeling (Table 4). Five days after labeling, the branch δ^{13}C of *Populus davidiana* and *Quercus wutaishanica* were higher than other sampling times. Twenty-one days after labeling, the leaf, branch, and root δ^{13}C of *Quercus wutaishanica* were 94%, 121%, and 35% higher than those of *Populus davidiana*, respectively. For both *Populus davidiana* and *Quercus wutaishanica*, the δ^{13}C of soil at 0–10 cm reached a peak 5 days after labeling (Table 4).

3.2. ^{13}C in soil, microbial biomass and extractable organic matter

In the case of both *Populus davidiana* and *Quercus wutaishanica*, the ^{13}C content in SOC in the 0–10 cm soil layer reached a maximum 5 days post-labeling and significantly higher than other sampling times (Fig. 2, $p < 0.05$). At 21 days after labeling, ^{13}C contents in the 0–10 cm and 10–20 cm layers of bulk soil and rhizosphere soil under *Quercus wutaishanica* were 58%, 72%, and 22% higher than those under *Populus davidiana*, respectively. In the 0–10 cm soil depth, the ^{13}C content in MBC was increased with the time after pulse labeling (Fig. 3, $p < 0.05$). With respect to rhizosphere soil, the ^{13}C content of MBC at 21 days after labeling for *Quercus wutaishanica* was 6.5% higher than that for *Populus davidiana* ($p < 0.05$). Whereas for both tree species, the ^{13}C content in extractable organic C at 12 days was higher than that at other sampling times.

3.3. ^{13}C recovery in the tree-soil-microorganisms system

The ^{13}C recovery in leaves decreased from 89% immediately after labeling to 40% at 21 days after labeling in *Populus davidiana,* and from 88% to 45% in *Quercus wutaishanica* (Fig. 4). In contrast, the ^{13}C recovery in branches increased from 10% immediately after labeling to 50% in *Populus davidiana* and from 10% to 40% in *Quercus wutaishanica* at 21 days after labeling. Similarly, in *Populus davidiana*, the ^{13}C recovery in roots increased from 0.4% at day 0 after labeling to 9.5% 21 days after labeling and in *Quercus wutaishanica* increased from 1.5% to 15%. According to first-order exponential decay functions, the ^{13}C recoveries in the leaves of *Populus davidiana* and *Quercus wutaishanica* at half-life were 40% and 37%, respectively (Fig. S2). The relationships between the ^{13}C recoveries in leaves and roots, and leaves and soil are shown in Fig. 5. Finally, we determined the relationships between the

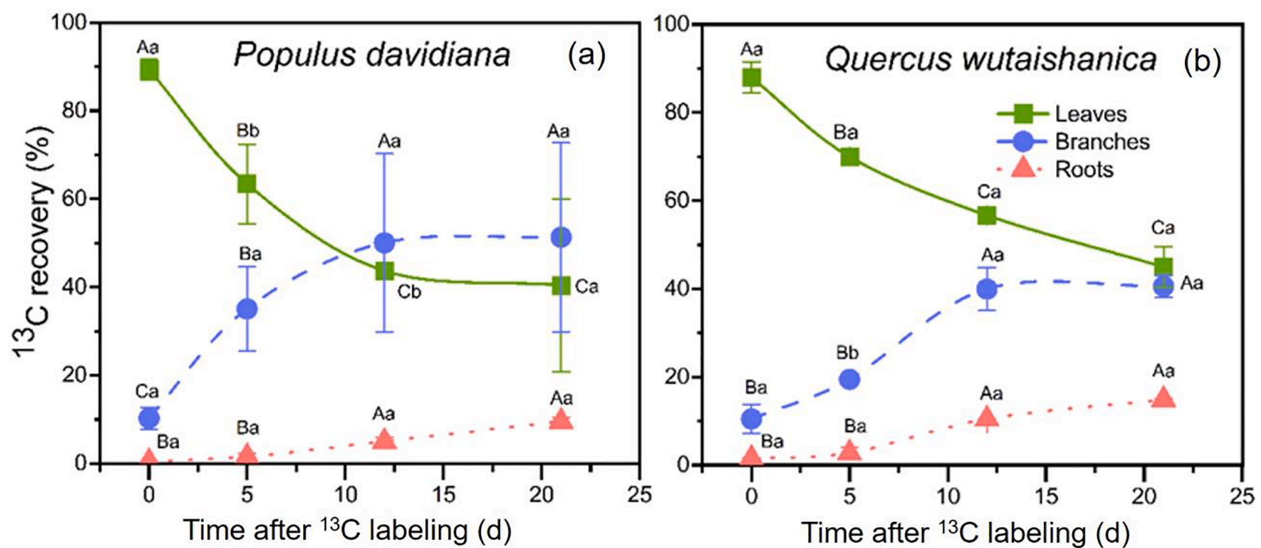

Fig. 4. ^{13}C amounts recovered from the leaves, branches, and roots of *Populus davidiana* and *Quercus wutaishanica* at 0, 5, 12, and 21 days after pulse labeling in a $^{13}CO_2$ atmosphere. Values are the averages (±SD) of three replicates. Lowercase letters (a, b, and c) indicate significant differences ($p < 0.05$) between two tree species at the same sampling time, and uppercase letters (A, B, and C) indicate significant differences ($p < 0.05$) at different sampling times for the same plant component (leaves, branches, or roots). *Note*: Day 0 corresponds to 6 h after the commencement of $^{13}CO_2$ labeling.

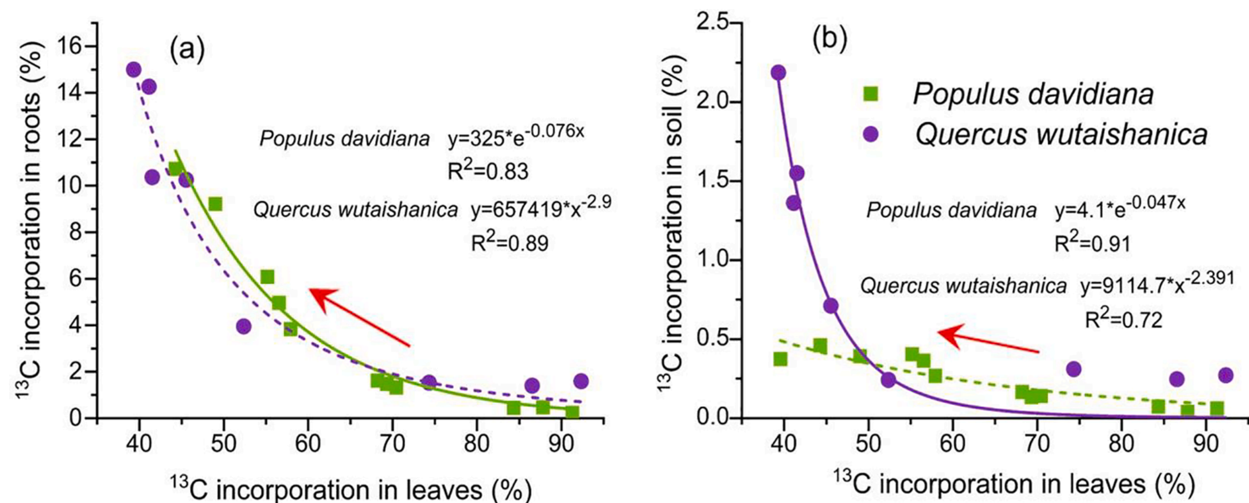

Fig. 5. Correlations between the allocation of recently assimilated C (^{13}C) to leaves, roots, and soil for *Populus davidiana* and *Quercus wutaishanica*. The red arrows show the direction of time after the ^{13}C labeling. Despite C allocation from leaves to roots is very similar between two tree species (left), the C allocation from leaves to soil (right) is much less for pioneer species *Populus davidiana* compared to climax species *Quercus wutaishanica*.

recoveries of ^{13}C from soil and roots for the two tree species (Fig. 6).

4. Discussion

4.1. Carbon allocation to the above- and below-ground parts of trees

During the past decade, considerable attention has focused on C turnover in soils under tree species (Högberg and Högberg, 2008; Keel et al., 2012; Sommer et al., 2017). We quantified the link between canopy assimilation and belowground processes, and traced the C flux into plant tissues and surrounding soil of the pioneer species *Populus davidiana* and climax species *Quercus wutaishanica* based on ^{13}C labeling. Overall, these two species differed markedly with respect to the assimilation rate and translocation of recently assimilated C to the soil. Compared with *Populus davidiana*, *Quercus wutaishanica* had assimilated twice the amount of applied $^{13}CO_2$ into leaves, branches and soil at 6 h after pulse labeling, which supported the first hypothesis stating that the climax species would fix more photosynthetic C, leading also to higher rhizodeposition. Differences between the two species regarding initial $^{13}CO_2$ uptake reflect the more rapid photosynthate transport in *Quercus wutaishanica* than in *Populus davidiana*. During the 6-h period of pulse-labeling, the CO_2 concentration and temperature within the labeling chambers were similar to those detected by an infrared CO_2 analyzer. The net photosynthetic rate, which is mainly determined by leaf stomatal conductance and intercellular CO_2 concentrations, was higher in *Quercus wutaishanica* leaves ($p < 0.05$) than in the leaves of *Populus davidiana* (Qin and Shangguan, 2006). The leaf chlorophyll content, the primary pigment used for the conversion of light energy to chemical energy was higher in *Quercus wutaishanica* than in *Populus davidiana* (Gitelson et al., 2003; Qin and Shangguan, 2006). Furthermore, we established that the N and P contents of *Quercus wutaishanica* leaves were higher than those in *Populus davidiana* (Table. 3), which would thus contribute to a higher net photosynthetic rate by affecting both photoreactive and dark reactive processes (Archontoulis et al., 2012; Miner

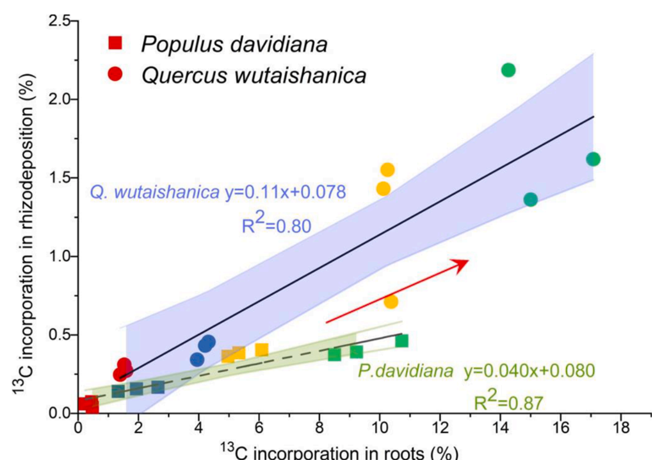

Fig. 6. Effect of ^{13}C in root biomass on rhizodeposition (^{13}C% of total assimilated ^{13}C) in the soil under *Populus davidiana* and *Quercus wutaishanica*. The shaded areas indicate the 95% confidence interval. The regression lines are significant at $p < 0.01$. The regression lines show that 11% and 4.0% of root C for climax species *Quercus wutaishanica* and pioneer species *Populus davidiana*, respectively, are released into soil as rhizodeposits. *Note*: The black, red, blue, and green squares and circles represent the data at 0 (6 h), 5, 12, and 21 days after the labeling of *Populus davidiana* and *Quercus wutaishanica*, respectively. The red arrow shows the direction of time after the ^{13}C labeling.

and Bauerle, 2019). Consistent with this assumption, we detected higher levels of $\delta^{13}C$ in the leaves and branches of *Quercus wutaishanica* than those of *Populus davidiana* at 21 days after labeling. Moreover, the measured differences in leaf $\delta^{13}C$ between labeled and control *Populus davidiana* were smaller than the values obtained for *Quercus wutaishanica* (Table.4), thereby indicating that the root $\delta^{13}C$ of the climax species increased to a greater extent than in the pioneer species via the transformation of C from leaves and branches.

Compared with *Populus davidiana*, the C allocated to the soil under *Quercus wutaishanica* contained twice the ^{13}C amount at 21 days after labeling, which again confirms the first hypothesis (Figs. 2 and 3). The average proportion of C allocated to the leaves of *Populus davidiana* and *Quercus wutaishanica* was 88% and 89% of newly fixed ^{13}C within the first 6 h, respectively (Fig. 4). However, at 21 days after labeling, the recovery of ^{13}C in belowground parts was 10% and 15% in *Populus davidiana* and *Quercus wutaishanica*, respectively, thereby indicating a more efficient belowground transfer of photosynthetic C in the climax species. The ^{13}C content in the EOC and MBC of soil under *Quercus wutaishanica* were considerably higher than those in soil under *Populus davidiana*, thereby indicating that the acquisition of exudates by microorganisms associated with the former species was more rapid than that in the latter (Kuzyakov and Domanski, 2002). The successional transition from pioneer *Populus davidiana* to a climax vegetation dominated by *Quercus wutaishanica* occurs at the Loess Plateau over a period of approximately 50 years. The relatively long-time span is required before these forests can act as C sinks, owing to a lack of soil disturbance during forest growth and the multistory structure both above- and belowground (Guo and Gifford, 2002; Deng et al., 2014; Song et al., 2020; Bai et al., 2020). Consequently, a higher plasticity with respect photosynthate rate and belowground C allocation could explain why climax species, being superior to “inhabitants” during revegetation, can outcompete other more rapidly growing species in terms of the acquisition of light and nutrients.

4.2. Allocation of C within the trees

Although we detected clear difference between the pioneer and climax species with respect to the rate of C transport, the results obtained

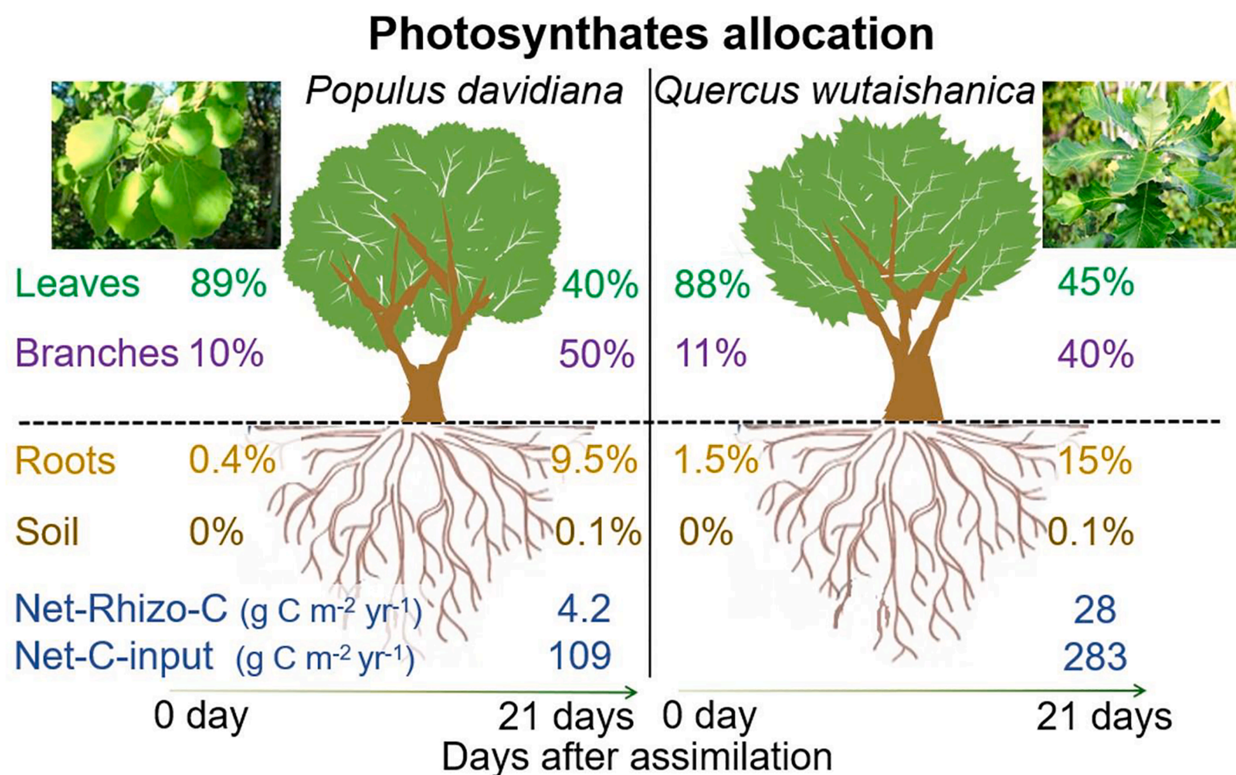

Fig. 7. Allocation of photosynthetically fixed C in a plant–soil system, as a percentage of the total ^{13}C assimilated by leaves, shoots, roots, and bulk soil, as well as rhizosphere soil, depending on the sampling time after labeling. The numbers in green, violet, yellow, and earthy yellow represent the C allocated to leaves, shoots, roots, and soil, respectively. Arrows at the bottom represent sampling time (days after labeling). The left- and right-hand panels show the data obtained for pioneer species *Populus davidiana* and climax species *Quercus wutaishanica*, respectively *Note*: Day 0 corresponds to 6 h after the commencement of $^{13}CO_2$.

for both species would tend to indicate a relatively rapid transfer of recently assimilated C to the soil. Recently assimilated C was detected in SOC immediately after labeling, which is consistent with our second hypothesis and also with the findings of other studies (Högberg and Högberg, 2008; Epron et al., 2011). The provision of C to roots via the transport of photosynthates is a major contributor to soil C pools, particularly MBC and EOC (Amiotte-Suchet et al., 2007). Although the leaves and branches are the major C sinks, a considerable amount of newly assimilated C was also allocated to the belowground (10%–15% at 21 days after labeling, Fig. 7). However, the belowground allocations are lower than those reviewed for grasslands and crops (Pausch and Kuzyakov, 2018; Wang et al., 2021). This is explained by the general stability of long-established forest root systems (Riederer et al., 2015) and the slower root turnover of trees (Freschet et al., 2013), which reflect a relatively low ^{13}C recovery in belowground pools.

According to Pausch and Kuzyakov (2018), at the half-life period of ^{13}C, the proportions of assimilated C remaining in the leaves of *Populus davidiana* and *Quercus wutaishanica* were 40% and 37%, respectively (Fig. S2). The corresponding proportions of assimilated C remaining in the roots and soil were 17%, and 1.6% and 16% and 0.6% of *Populus davidiana* and *Quercus wutaishanica*, respectively (Fig. 5). The relationships between the ^{13}C in roots and soils show that 4.0% of root C in *Populus davidiana* and 11% of root C in *Quercus wutaishanica* were released into the soil as rhizodeposits (Fig. 6). The ratio of the total assimilated photosynthetic C to exudation C in *Quercus wutaishanica* was higher than in *Populus davidiana*, which supported the first hypothesis. These proportions are smaller than those reported in previous pulse labeling studies that have focused on grasslands and crops (Zang et al., 2019; Liu et al., 2019). Although root-derived C has been established to be the main source of SOC in grasslands and crops, litter-derived C makes a greater contribution to SOC in forests than root-derived C (Berg, 2000; Freschet et al., 2013). The timescale of the transfer of root C to soil in forests tends longer than that in grasslands and crops, as it is estimated that the average forest root turnover is 5.3 and 5.5 times lower than that of grasslands and crops globally (Gill and Jackson, 2000). Further studies are needed to explore the factors that influence the ratio of the rhizodeposition C to root C. Although C allocation within the plant–soil system is influenced by multiple factors (Jones et al., 2009), the newly assimilated ^{13}C in soil was positively correlated with that assimilated by roots in both *Populus davidiana* and *Quercus wutaishanica*. This finding is consistent with observations in crops (Zang et al., 2019) and pastures (Wilson et al., 2018), which indicate that ^{13}C recovered in the rhizosphere is dependent to a greater extent on the release of C from roots than on the photosynthesis rate (Remus et al., 2016).

On the basis of the relationship between the ^{13}C incorporated into roots and soil, it is possible to gain a rough estimation of net C rhizodeposition on a field scale in forests. According to the findings reported by Sun (2018) and Deng (2015), the annual root biomass for young *Populus davidiana* and *Quercus wutaishanica* was 240 and 560 g m^{-2}, and that C in the root biomass was 105 and 255 g m^{-2} yr^{-1}, respectively. The average growing season of forests on the Loess Plateau is approximately 150 days (Liu, 2003). Based on the relationship between the roots of 5-year-old *Populus davidiana* and *Quercus wutaishanica* and rhizodeposition in the upper 20 cm layer of soil, the net C input via rhizodeposition was 4.2 and 28 g C m^{-2} yr^{-1}, respectively (detailed calculations are shown in the Supplementary materials). Such large differences in rhizodeposition are conceivably attributable to the differing ecological strategies of these plant species with respect to growth, reproduction, and resource acquisition (Kaštovská et al., 2017). The net effect of plant growth on SOC dynamics reflects the balance between plant C input and native SOC mineralization (Lu et al., 2002). Thus, the actual net rhizodeposition is lower than the C allocated to the roots, which we calculated according to the relationship between rhizodeposition and roots. Taking into consideration both the root and rhizodeposited C in soil to a depth of 20 cm, the net belowground C input by *Populus davidiana* and *Quercus wutaishanica* amounted to 109 and 283 g C m^{-2} yr^{-1}, respectively, (Fig. 7). The net C input via rhizodeposition accounting for 3.9% and 10% of the net belowground C (rhizodeposition C + root C) of *Populus davidiana* and *Quercus wutaishanica*, respectively.

The major uncertainty in our estimates is that root turnover in *Populus davidiana* and *Quercus wutaishanica*, along with the decomposition of rhizodeposits, were not considered (Kuzyakov, 2011; Pausch and Kuzyakov, 2018). Moreover, we only obtained the net belowground C and net C input via rhizodeposition to the initial 21 days after photassimilation. Consequently, it would be necessary to conduct either continuous labeling or multiple pulse labeling to facilitate evaluations of the effects of seasonal changes on C allocation and stabilization in soil.

5. Conclusions

The allocation of photosynthetic C in plant–soil–microorganisms and estimated quantity of net C input by trees via rhizodeposition were done based on ^{13}C pulse labeling. Photoassimilates in the pioneer species *Populus davidiana* and climax species *Quercus wutaishanica* were transferred through branches to roots within a few days and were subsequently rapidly distributed within the soil pools. At 6 h post-labeling, ^{13}C amounts in the leaves of *Quercus wutaishanica* were approximately two-fold larger than those in the leaves of *Populus davidiana*. The ^{13}C recovery in leaves decreased but in branches and roots increased from 6 h to 21 days after assimilation. Similarly, the ^{13}C contents in soil organic carbon, microbial biomass, and extractable organic C under climax species *Quercus wutaishanica* were two-fold larger than those in pioneer species *Populus davidiana*, thereby indicating a more rapid utilization of the root-derived organic compounds by the climax species. Consequently, plant and soil C stocks will increase in forest systems with a transition from pioneer to climax species dominance. The net belowground C input (in roots and soil) from 5-year-old *Populus davidiana* and *Quercus wutaishanica* trees amounted to 109 and 283 g C m^{-2} yr^{-1}, respectively, including 4.2 and 28 g C m^{-2} yr^{-1} net rhizodeposited C in 0–20 cm soil depth, respectively. These results provide direct evidence that soil C sequestration would increase with the successional transition from pioneer to climax tree species.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2021.115296.

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